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Centipede diversity in patches of different development phases in an unevenly-aged beech forest stand in Slovenia

by

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ABSTRACT

The issue investigated was whether a distinction can be made between centipede communities from different development phases of an unevenly-aged beech forest stand. The influence of stand structure on centipede diversity, resulting from a particular forest management practice, was evaluated. Soil samples were taken three times during 2000 from a beech stand with patches of different development phases near Ljubljana in Slovenia. Using the quadrat counts method, soil samples were taken with a sampling corer from adjoining selected patches in understorey re-initiation (gap-patch), juvenile, pole and timber phases of a forest. The characteristics of centipede communities and the similarities between them were then estimated by use of statistical methods (Jackknife estimate of species richness, Shannon-Wiener diversity index, Pielou's index of evenness, index of dominance, Renkonen index). The collection comprised 2075 centipedes representing 36 species. In a single patch, 24–28 species were found. Average centipede density was between 109 and 892 individuals per square metre. None of the common species was found exclusively in one development phase. The responses to forest development phases differed among species. Some species were considerably more abundant in older forest development phases, but most species did not show preference for a certain development phase. Differences between patches lay mostly in the distribution and abundance of species. Some samples from different patches are more similar than seasonal samples taken from the same patch. It was discovered that the centipede community structure in patches of an unevenly-aged stand does not only depend on a forest development phase. The inference was made that centipedes migrate between patches with different environmental conditions. Such an unevenly-aged stand can offer favourable conditions for more centipede species, so it was predicted that both alpha diversity and density are higher than they would be in an evenly-aged stand in the same area. Since small-scale heterogeneity within a forest stand enhances local species richness and supports viable populations of specialised species, maintenance of this heterogeneity should be the key focus in management operations within a forest stand.

INTRODUCTION

The diversity of forest soil fauna in managed forests depends on management practices. In current forest management, emphasis is placed not only on timber production but also on other values (Kangas *et al.* 1993). Satisfying the main needs of wildlife populations is one of these. Since most processes in an ecosystem are led by organisms, biodiversity plays a key role in healthy forest functioning. Conservation of biodiversity is one of the main criteria for contemporary multiple-use, sustainable and ecosystem forest management. Slovenia is obliged to conserve and investigate biodiversity under international agreements and its own legislation.

Forest management practices alter forest composition, structure and spatial heterogeneity, thereby often changing temporal and spatial wildlife diversity and abundance (Wigley & Roberts 1994). Animal populations are being increasingly fragmented into separated local populations that behave according to the principles of metapopulation ecology (Hanski & Gilpin 1997). Extinction and colonisation dynamics are becoming ever more distinctive, and the importance of migration is increasing. Hanski (1998) noted that the size and optimal spacing of preserved habitat fragments, along with organisms' migration possibilities, are very important for reducing the negative effects of fragmentation. We suggest that this could also ease the negative effects of homogenisation.

During its dynamic existence, a forest passes through several development phases. Since canopy closure, as well as illumination, temperature, humidity and other abiotic factors are different (Barnes *et al*. 1980; Caldwell & Pearcy 1994), there are wide variations in conditions during different development phases. Researchers have considered the influence of different development phases on fauna. In different forest development phases, communities of springtails (Setäla & Marshall 1994), carabids (Niemelä *et al*. 1996), spiders (Niemelä *et al*. 1996), ants (Niemelä *et al*. 1996), bark beetles (Mokrzycki 1995) and other groups of soil fauna, along with vertebrates (e.g. Carey & Johnson 1995), have been investigated. Differences between phases were found, but few species from different animal groups were found only in certain phases, and most of them were common to several phases.

In recent years, the search for indicators enabling us to clearly understand what is happening in the whole community has expanded. Noting the characteristics of a good indicator (Favila & Halffter 1997), we inferred that centipedes could be an appropriate indicator of biodiversity in Slovenian forest soils. They have the following characteristics that allow them to be an indicator taxa:

1. There is sufficient information available on the behaviour, ecology, taxonomy and phylogeny of centipedes.
2. As macroarthropod predators, centipedes are a very important group of soil fauna (Albert 1979; Fründ 1983; Kos 1995*a*).
3. In a given geographical region, centipede communities in forest soils strongly differ from those in non-forest areas (Kos 1988 1996; Grgič 2002).
4. Centipedes are easy to capture, and sampling methods are easily repeatable (Kos 1988).
5. Capture data provide enough information to determine the composition and structure of the centipede community and its interaction with other groups.
6. Wide geographical distribution: centipedes occur on almost all continents, except for Antarctica (Grgič 1999).
7. In Slovenia, the centipede fauna is rich, with more than 90 species already known (Kos 1992).
8. Centipede abundance is great (Kos 1996; Grgič 2002). Centipedes are the most numerous macroarthropod predators of soils in Slovenia (Kos & Praprotnik 2000).
9. Collecting centipedes for research purposes cannot threaten populations in Slovenia.

We suggested that centipede diversity depends on a stand’s age and horizontal structure since environmental conditions in a forest undergo changes during its development. We investigated centipede communities in patches of different development phases in an unevenly-aged stand. Attempts were made to investigate whether they differ from each other, to evaluate the dependence of centipede community structure on a forest development phase, and to state the suitability of heterogeneous stand structure for centipede diversity. The results of such ecological investigations in different animal and plant groups should serve as a basis in selection of appropriate forestry practices that would assure sustainable existence of forest.

MATERIALS AND METHODS

Study sites

The study site was a 16 ha, unevenly-aged beech stand in Dinaric forests located near Iška, a village 15 km south of Ljubljana in Slovenia. Soil samples were taken from four 0.25–0.5 ha sized patches of different development phases: re-initiation, juvenile, pole and timber phase. The site is on a north-western aspect at altitudes from 409 to 455 m with 15–25 cm deep brown soil on limestone geological foundation. The re-initiation phase (45°54'44"N, 14°30'39"E) is the initial development phase under the canopy gap, overgrown by herbs, and without trees. The juvenile phase (45°54'48"N, 14°30'37"E) is the young development phase with middle stem diameter of up to five centimetres. Tree canopy closure is complete. The pole phase (45°54'48"N, 14°30'38"E) is a somewhat older development phase, with middle stem diameter from 10 to 15 centimetres, and smaller separate gaps between canopies. The oldest development phase we investigated was the timber phase (45°54'45"N, 14°30'39"E), with the middle stem diameter over 30 cm, and bigger gaps between canopies. Distances among sampling sites were from 30 to 350 m.

Sampling and material treatment

Soil samples were taken using the method of quadrat counts, with a 21 cm diameter sampling corer, approximately 15 cm deep in the soil. Sample units also include litter and the fermentative horizon. In each study patch within a 15x15 m quadrat we took nine sampling units, evenly distributed over the quadrat. Samples were collected three times in 2000: 6 June (spring), 5 September (summer), and 21 December (autumn).

Sample units were then separately extracted using Tullgren funnels, modified so that the lower parts of funnels were cooled. Animals were intercepted in vessels with Ethylene Glycol. The extraction lasted 21–30 days.

For centipede identification we used various taxonomic texts (e.g. Eason 1964 1982; Koren 1986 1992; Matic 1966 1972; Verhoeff 1931 1937).

The material collected in the study is part of the centipede collection of the Department of Biology at Biotechnical Faculty, Ljubljana (Iška, T001-T680).

Statistical analysis

We used standard indices employed in faunistic and soil zoology studies. For density and distribution estimates, we used the method of quadrat counts (Krebs 2000). Using the Jackknife method, we estimated species numbers in communities ($\hat{S}$). We calculated Shannon-Wiener diversity indices (H') and Pielou's indices of evenness ($J'=H'/H'_{\mathrm{MAX}}$) (Krebs 2000). Based on index of dominance ($x_I = (n_i/N)100(\%)$; where n_i = number of individuals of a particular species in the sample, N = number of all individuals in the sample), we identified the degree of dominance for individual species (more than 10 % = eudominant species; 5–10 % = dominant species, less than 5 % = subdominant species) (Tarman 1992).

We calculated similarity among centipede communities using percentage similarity (Renkonen index) (Krebs 1989 2000). We prepared a dendrogram of similarity using the UPGMA method of clustering as performed by PHYLIP (Felsenstein 2002). It constructs a tree by successive (agglomerative) clustering using an average-linkage method of clustering. As distances among centipede community samples, we used d (d=1-percentage similarity).

TABLE 1.

Occurrence of centipede species, their average densities and distribution (C = clumped, R = random) in study patches in an unevenly-aged beech stand at Iska (Slovenia), based on soil samples of 2000.

species	**re-initiation phase**			**juvenile phase**			**pole phase**			**timber phase**		
	average density (ind./m^2)			average density (ind./m^2)			average density (ind./m^2)			average density (ind./m^2)		
	spring	summer	autumn	spring	summer	autumn	spring	summer	autumn	spring	summer	autumn
Brachyschendyla montana (Attems, 1895)			6.4	3.2		9.6			22.5		3.2	16.0
Clinopodes flavidus C. L. Koch, 1847	3.2	3.2					12.8			22.5	16.0	
Clinopodes sp.	25.7	6.4		35.3	25.7		32.1	6.4		41.7	3.2	3.2
Cryptops hortensis Leach, 1815	44.9	70.6	48.1	35.3	54.5	93.0	54.5	9.6	28.9	105.9	83.4	54.5
Cryptops parisi Brolemann, 1920	16.0	6.4	19.2	12.8	12.8	9.6	25.7	3.2	28.9	12.8	3.2	25.7
Dicellophilus carniolensis C. L. Koch, 1847	9.6	3.2	16.0	3.2	3.2		6.4			3.2		
Eupolybothrus tridentinus (Fanzago, 1874)						3.2			3.2			
Geophilus cf. *abbreviatus* Verhoeff, 1925	3.2	3.2				3.2			3.2			
Geophilus electricus (Linnaeus, 1758)			3.2	3.2		12.8					3.2	16.0
Geophilus flavus (De Geer, 1778)	3.2	9.6		19.2	3.2					6.4	28.9	
Geophilus insculptus Attems, 1895	12.8	9.6	16.0	9.6	3.2	9.6	6.4	6.4	16.0		12.8	9.6
Geophilus cf. *larii* Verhoeff, 1934	160.4	99.4	64.2	170.0	109.1	64.2	109.1	35.3	35.3	118.7	157.2	73.8
Geophilus sp. E										3.2		
Harpolithobius sp.	6.4		6.4	12.8	9.6	16.0	3.2			9.6		
Henia illyrica (Meinert, 1870)	6.4											
Lithobius agilis C. L. Koch, 1847				3.2		3.2						
Lithobius castaneus Newport, 1844				3.2	6.4	3.2	9.6		3.2			
Lithobius dentatus C. L. Koch, 1884	3.2	3.2							3.2		6.4	3.2
Lithobius lapidicola Meinert, 1872	6.4	6.4	3.2			3.2	6.4	3.2	6.4	6.4	3.2	6.4
Lithobius latro Meinert, 1872	9.6	6.4	3.2		6.4	3.2				6.4	3.2	3.2
Lithobius cf. *lucifugus* L. Koch, 1862						3.2						

TABLE 1 (continued).

species	**re-initiation phase**			**juvenile phase**			**pole phase**			**timber phase**		
	average density (ind./m^2)			average density (ind./m^2)			average density (ind./m^2)			average density (ind./m^2)		
	spring	summer	autumn	spring	summer	autumn	spring	summer	autumn	spring	summer	autumn
Lithobius cf. *melanops* Newport, 1845			3.2					3.2		9.6		3.2
Lithobius nodulipes Latzel, 1880				3.2	6.4		6.4		3.2			
Lithobius pygmaeus Latzel, 1880	61.0	38.5	32.1	6.4	22.5	9.6	118.7	6.4	51.3	48.1	86.6	9.6
Lithobius tenebrosus Meinert, 1872	3.2											
Lithobius validus Meinert, 1872				3.2								
Lithobius (*M.*) sp. A							3.2			6.4		
Lithobius (M.) aeruginosus L. Koch, 1862	28.9	57.7	35.3		3.2		57.7		9.6	35.3	28.9	19.2
Lithobius (M.) sp. D	3.2			3.2						12.8		
Lithobius (*S.*) sp.	77.0	83.4	32.1	44.9	32.1	64.2	93.0	3.2	41.7	170.0	170.0	80.2
Lithobius (S.) carinthiacus Koren 1992	67.4	25.7	12.8	64.2	19.2	73.8	118.7	12.8	32.1	38.5	22.5	
Schendyla carniolensis (Verhoeff, 1902)			9.6		9.6	9.6					3.2	3.2
Schendyla cf. *nemorensis* (C. L. Koch, 1836)		6.4										
Strigamia acuminata (Leach, 1815)	6.4	3.2		6.4		6.4	6.4	6.4	19.2	6.4	6.4	6.4
Strigamia crassipes (C. L. Koch, 1835)						3.2	6.4				6.4	
Strigamia transsylvanica (Verhoeff, 1928)	6.4		9.6	3.2	6.4	6.4	12.8			9.6	6.4	6.4
Geophilus sp.	6.4											
Lithobius juven.	102.7	160.4	105.9	44.9	80.2	102.7	202.1	6.4	102.7	118.7	189.3	86.6
Lithobius sp.	16.0	12.8	3.2		3.2			3.2			12.8	3.2
Harpolithobius juven.				3.2		3.2		3.2	3.2			
Total density	**689.7**	**609.5**	**436.3**	**494.0**	**417.0**	**516.5**	**891.8**	**109.1**	**413.8**	**792.4**	**856.5**	**429.9**
Distribution	**C**	**C**	**R**	**R**	**C**	**C**	**C**	**R**	**C**	**C**	**C**	**C**

RESULTS

We collected 2075 centipedes representing 36 species (Table 1). We found five species new to science: *Clinopodes* sp. (all phases), *Geophilus* sp. E (timber phase), *Lithobius* (*Monotarsobius*) sp. A (pole and timber phases), *Lithobius* (*Monotarsobius*) sp. D (all phases except the pole phase), and *Lithobius* (*Sigibius*) sp. (all phases).

We found the largest number of species in the juvenile phase (28), followed by the re-initiation phase (27), the timber phase (26), and the fewest in the pole phase (24). In spring, the highest number was found in the re-initiation phase, followed by the juvenile and timber phases, and the lowest in the pole phase. In summer, the greatest number of species was found in the timber phase, with the juvenile and re-initiation phases following. In autumn, the highest number of species was in the juvenile phase. In the pole and re-initiation phases, the number of species was highest in spring, while in the juvenile phase it was highest in autumn. In the juvenile, pole and re-initiation phases, the lowest number of species was found in summer (Table 2).

In spring, we found the largest number of centipedes in the pole phase, but the smallest in the juvenile phase. In summer, the largest number of specimens was located in the timber phase, followed by the re-initiation and juvenile phases, and very few in the pole phase. In autumn, the number was highest in the sample from the juvenile phase. Centipede density in a single patch varied during the year. In the pole and juvenile phases, centipede density was lowest in summer. In the timber phase it increased until summer but then significantly decreased until autumn. In the re-initiation phase, centipede density fell from spring to autumn (Table 2).

All samples included in this study were very similar to each other (percentage similarity) (Fig. 1). Some samples from different phases were more similar to each other than samples from the same phase. In terms of similarity, samples from a single phase cannot be strongly separated from others. When we joined all three samples from a single phase together, the phases were more similar to each other (69–79 % similarity) than they were at a particular time of the year (in spring 56–78 %, in summer 51–80 %, in autumn 58–70 %) (Table 3).

Most species occurred in all four patches. Species not found in all patches were represented by a very low number where they were recorded. Differences between

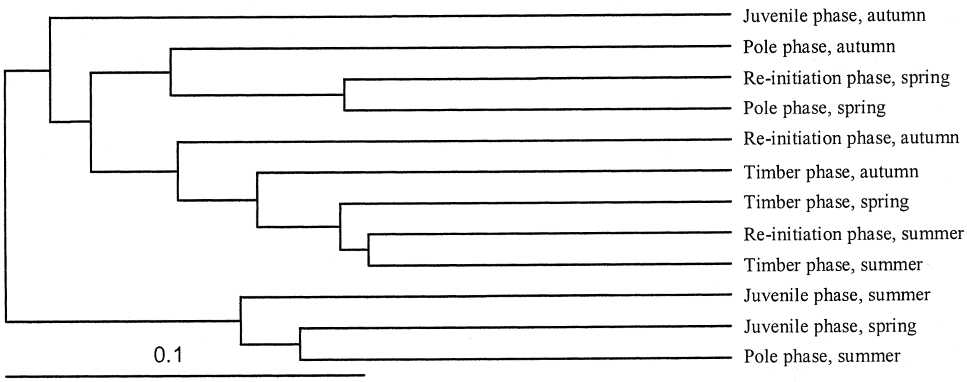

Fig. 1. Dendrogram of similarities among centipede community samples from different forest development phases, sampled in three different periods in 2000 (distances calculated as (1-percentage similarity)).

patches lay not in the presence or absence of species, but in their distribution and abundance. Three species were represented by considerably smaller number of specimens in samples from younger forest development phases than in samples from older ones: *Clinopodes flavidus* (in the re-initiation phase two specimens, in the pole phase four, and in the timber phase 12), *Lithobius* (*Monotarsobius) aeruginosus* (in the juvenile phase one specimen, in others more than 20), *Lithobius pygmaeus* (in the juvenile phase 12 specimens, in others more than 40). The number of *Dicellophilus carniolensis* specimens caught dropped with forest age (in the re-initiation phase nine specimens, in the juvenile and pole phases two specimens, but in the timber phase only one). For the majority of species, we cannot determine from our data which development phase they prefer, since insufficient specimens were collected to allow such an inference.

Using the method of quadrat counts (Krebs 2000) we estimated that centipedes in the studied patches were distributed in clumps or randomly, and never uniformly (Table 1).

Characteristics of centipede communities in individual forest development phases

Re-initiation phase

In samples taken from the re-initiation phase, 27 species are represented by 541 centipedes, with 215 specimens (22 species) in the spring sample, 190 (17 species) in the summer sample and 136 (18 species) in the autumn sample (Tables 1–2). Average density estimates were between 436 and 690 ind./m^2. In the spring and autumn, centipedes were distributed in clumps, while in autumn their distribution was random. The evenness of a centipede community was higher in autumn than in previous samples (spring and summer) and so was the Shannon-Wiener index, although the community supported the highest number of species in spring. In autumn, the chilopod community in the re-initiation phase had the highest values of Shannon-Wiener index among all the communities studied (Table 2).

Juvenile phase

Of 445 centipedes involving 28 species, 154 (20 species) were caught in spring, 130 (17 species) in summer and 161 (21 species) in autumn (Tables 1–2). In summer and autumn, centipedes were distributed in clumps. Average-density estimates were between 417 and 516 ind./m^2. Diversity (*H’*) of the community increased during the year, but not strongly (from 3.03 to 3.37) (Table 2).

Pole phase

Samples taken from the pole phase contained 441 centipedes representing 24 species. In spring 19 species were represented by 278 specimens, in summer there were 11 species with only 34 specimens, and in autumn 16 with 129 centipedes (Tables 1–2). For spring and autumn, the distribution was estimated as clumped, while in summer it was random. Average density estimates were between 109 ind./m^2 in summer and 892 in spring. The summer sample from this phase was the poorest of all the samples studied, in terms of both species number and number of specimens. This also resulted in the lowest Shannon-Wiener index value (2.95). The evenness of the community varied very little throughout the year (from 0.80 to 0.88). The diversity index (*H’*) value was relatively high for the community in autumn (*H’* = 3.52) (Table 2).

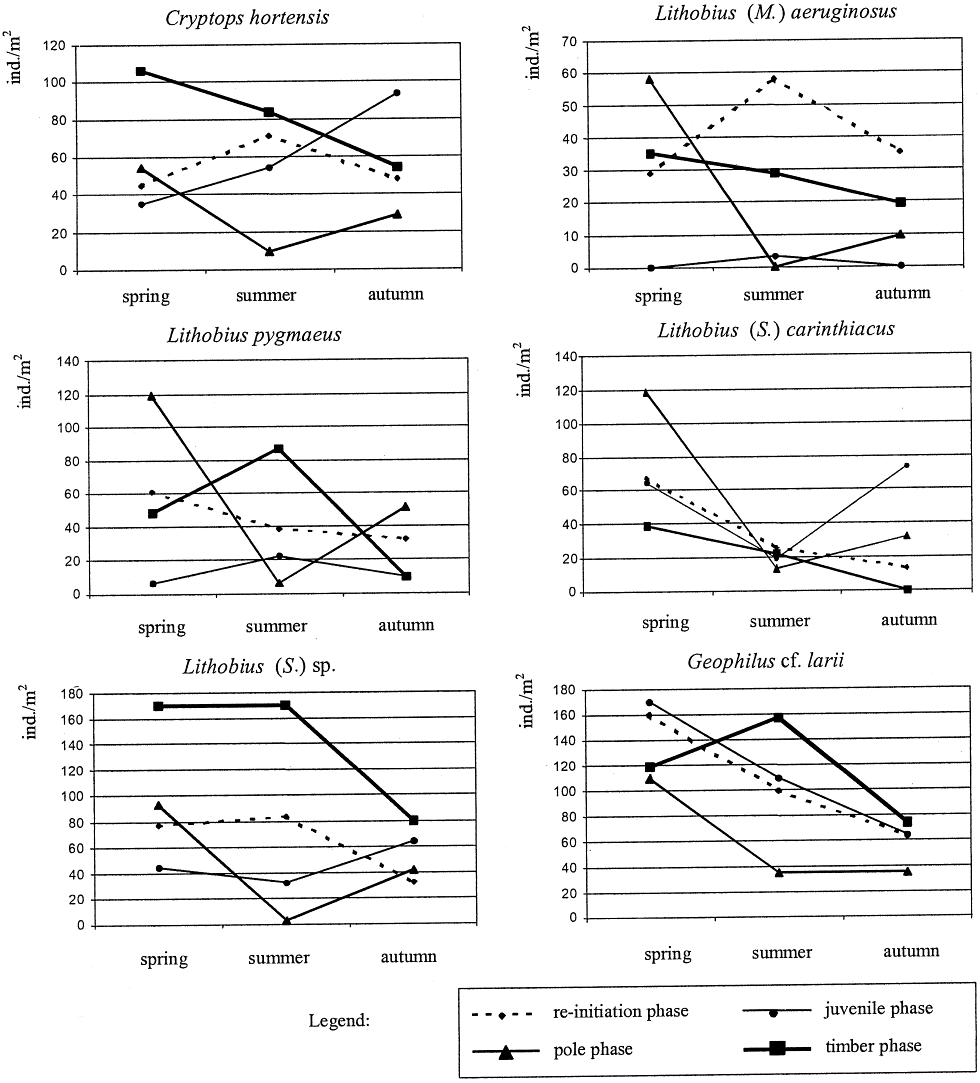

Fig. 2. Average density estimates of some centipede species from different development phases in an unevenly-aged beech stand at Iška (Slovenia), based on soil samples in 2000.

Timber phase

In samples from the timber phase 648 centipedes representing 26 species were sampled. These comprised 247 collected in the spring sample and 267 in the summer one (20 species in both), and 134 in the autumn sample (17 species) (Tables 1–2). Centipedes in this patch had a clumped distribution. Average density estimates were between 430 and 857 ind./m^2, with the highest occurring in summer. The values of both the evenness of the dominance distribution and the diversity index were very low for the summer community. Evenness was highest in autumn, yet the number of species was lowest. Consequently, the diversity index had a medium value (Table 2).

The occurrence of abundant species

The density of abundant species in a particular patch varied during the year (Table 1, Fig. 2).

Cryptops hortensis

In the spring the highest density estimate was made for the timber phase (105 ind./m^2) and it then decreased towards autumn, but stayed high. In samples taken from other phases, average densities in spring were much lower and did not differ much (35–55 ind./m^2). In summer, the density in the pole phase was still lower, while in the re-initiation and juvenile phases it increased. Until autumn, the average density of specimens in the re-initiation phase dropped, while strongly increasing in the juvenile phase. This species was eudominant in the timber phase, and, except for spring when it was dominant, also in the re-initiation and juvenile phases. In the pole phase, it was dominant.

Lithobius (*Monotarsobius*) *aeruginosus*

The average density was up to 57 ind./m^2, being highest in the pole phase in spring and in the re-initiation phase in summer. In the juvenile phase, only one specimen was found. In the re-initiation phase this species was dominant in spring, but eudominant in summer and autumn. In pole and timber phases it was subdominant to dominant.

Lithobius pygmaeus

In spring and autumn the density was highest in the pole phase, while in summer it was lowest there. Up until summer, the density strongly increased in the timber phase, also somewhat in the juvenile phase, but it was lowest in this patch. In the re-initiation phase, the density did not change much during the year. This species was eudominant in the pole phase and in summer also in the timber phase. It was dominant in the re-initiation phase.

Lithobius (*Sigibius*) *carinthiacus*

This species was most abundant in the pole phase in spring. In summer, the density estimates in different phases were very similar and low. Until autumn, the density increased again in the pole phase and in juvenile phase also, where it was highest at that time. It was eudominant in the re-initiation phase in spring and in the juvenile and pole phases in spring and autumn.

Lithobius (*Sigibius*) sp.

In the timber phase it was the most abundant species in the centipede community, and was eudominant. Average density was very high (170 ind./m^2) in spring and summer, while it dropped until autumn to half the value. Similarly, it occurred in the re-initiation phase, but its values were 50 % lower. In the pole phase, the number of specimens decreased in summer, yet increased again until autumn. It was eudominant in the re-initiation and juvenile phases and, excluding summer, also in the pole phase.

Geophilus cf. *larii*

This was the species with the highest average density estimates in the forest stand studied. The highest (up to 170 ind./m^2) were identified in the juvenile and re-initiation phases in spring, and they then decreased until autumn to 64 ind./m^2. In the timber

TABLE 2.

Principal characteristics of centipede communities in different development phases of an unevenly-aged beech stand at Iška (Slovenia), based on soil samples of 2000. Species number: in sample: number of species in the sample, estimate ($\hat{S}$): estimation of species number with Jackknife estimate, confidence interval: lower and upper 95 % confidence limits of species number. Density estimates using quadrat sampling method: average density, lower and upper 95 % confidence limits. Community indices: *H’*↓: Shannon-Wiener diversity index, *H’*↑max : maximal value of *H’*, *J’*: index of evenness.

development phase	sample	**species number**				**ind. numb.**	**density estimate**			**community indices**		
		(in sample)	**estimate ($\hat{S}$)**	confidence interval		(in sample)	**ind./m²**	confidence interval		*H’*	*H’*max	*J’*
re-initiation phase	*spring*	22	**28.2**	23.1	33.3	215	**689.7**	401.2	913.1	3.43	4.46	0.77
	summer	17	**21.4**	18.2	24.7	190	**609.5**	303.8	853.6	3.17	4.09	0.77
	autumn	18	**21.6**	18.3	24.8	136	**436.3**	360.0	515.6	3.62	4.17	0.87
juvenile phase	*spring*	20	**28**	19.9	36.1	154	**494.0**	412.9	578.3	3.09	4.32	0.72
	summer	17	**21.4**	15.2	27.7	130	**417.0**	183.7	615.4	3.24	4.09	0.79
	autumn	21	**28.1**	22.4	33.8	161	**516.5**	360.4	668.5	3.37	4.39	0.77
pole phase	*spring*	19	**21.7**	18.6	24.7	278	**891.8**	524.0	1177.6	3.41	4.25	0.80
	summer	11	**15.4**	11	19.9	34	**109.1**	76.2	150.8	2.95	3.46	0.85
	autumn	16	**20.4**	16	24.9	129	**413.8**	156.1	644.3	3.52	4.00	0.88
timber phase	*spring*	20	**24.4**	21.2	27.7	247	**792.4**	556.9	987.6	3.38	4.32	0.78
	summer	20	**27.1**	19.9	34.3	267	**856.5**	614.0	1065.7	3.10	4.32	0.72
	autumn	17	**23.2**	14.6	31.8	134	**429.9**	173.1	619.2	3.26	4.09	0.80

phase, the density increased until summer from 119 to 157 ind./m^2, but in autumn it fell again. In the pole phase, the highest density was found in spring. *Geophilus* cf. *larii* was the most abundant species in the re-initiation and juvenile phases, and eudominant in all phases.

DISCUSSION

Characteristics of the centipede fauna at the studied site

In the stand we studied we found 36 centipede species, while in similar forests in Middle Europe only some 15 species were found (Albert 1982; Fründ 1983). In the forests of the studied area, in addition to Middle European species, species that are typical of the Balkan Peninsula also occur (Grgič 1999; Kos & Grgič 2001). In this area they survived the glacial period in refuges (Kos 1992). Because of their low reproductive potential and several year long life cycles (Lewis 1965; Albert 1983; Radl 1992), centipedes generally have a low dispersal potential. The spatial expansion of centipede species is thus slow compared to plant species, which to the north probably already also present a potentially suitable environment for several Balkan centipede species (Grgič 1999). Another important reason for such a high species richness in the refuge area is the community's high age (Brewer 1994) and the coevolution of species. Heterogeneity of the Dinaric landscape and speciation in refuges are reasons why many endemic species of the broad Dinaric area occur there. The area is poorly investigated, therefore the discovery of five new centipede species there during this study was not surprising.

Average centipede densities in the studied unevenly-aged stand (109–892 ind./m^2) are much higher than previous estimations for centipede communities in the same geographical region (up to 580 ind./m^2) (Kos 1996; Kos & Praprotnik 2000). In general, the densities of centipedes in Slovenian forests are much higher than those in German forests (up to 171 ind./m^2) (Fründ 1983; Albert 1982) and those in England (Roberts 1957), Hungary (Loksa 1968) and Poland (Tuf 2000; Leśniewska 2000; Tracz 2000; Wytwer 2000), which do not exceed 430 ind./m^2, but are mostly around 100 ind./m^2. The high density of centipedes, and their high biomass, indicates the great significance of centipedes in the forest soils of Slovenia.

Centipede diversity in patches of different forest development phases

Our results confirm the identified differences in centipede communities from patches of different development phases in an unevenly-aged forest stand. Some species were more abundant in a defined development phase, but most occurred in all four patches. None of the abundant species was exclusive to one phase. Relative abundance varies more than species composition. We assume that canopy closure, and consequently illumination, temperature and humidity of the soil, is the key factor for species occurrence in a certain phase, since centipedes are sensitive to temperature (Grgič & Kos 2001) and dryness (Fründ 1983). Sensitivity differs among species (Grgič & Kos 2001). Less sensitive species are more tolerant of changes and probably occur in different environments, but those requiring particular environmental conditions occur in environments with defined characteristics. Successional change in forest structure is relatively rapid in the first years and decades following cutting, but slows down later on. The most favourable period for species of young successional stages is, accordingly, shorter than for species of older stages. However, it must be stressed that, besides abiotic factors, biotic factors such as competition, predation and others are also important influences, and this prevents us from directly linking centipede occurrence only with forest structure. A combination of all factors is important.

In a single phase, changes in density and species number during the year were great. Given the low reproductive potential of centipedes (Albert 1983; Radl 1992; Lewis 1965), these changes cannot be a consequence of reproductive processes. We deduct that centipedes migrate between patches. The existence of centipede migrations has already been mentioned by Kos (1995), Tracz (2000) and others. Because of small distances ranging from a few metres to some 10 metres, movements of centipedes among phases are possible. In addition, these movements are probably the reason why some samples from different phases are more similar than samples from the same phase collected in different periods of the year (Fig. 1).

In autumn centipedes were relatively uniformly distributed among patches of different successional stages of the studied beech forest. Conditions in different phases do not differ much in autumn since the trees are without leaves and this is probably why the preference of centipedes for a defined phase was not observable. Differences in centipede density among patches were greatest in summer when differences in environmental conditions among patches are also the greatest. Especially in the pole phase, both density and species number fell strongly until summer, while in spring in this phase alone the density was highest among the phases, which also leads to the presumption about migrations. Changes are small in the re-initiation phase. We expect that in a patch under a greater gap in the canopy, the density of centipedes and the number of species would drop in summer. However, the gap patch studied is too small to have significant consequences for centipedes. For most of the day it is in the shadow of timber-phase trees so the conditions do not differ strongly from those in the timber phase. The prediction was made that in a bigger gap patch, species of open areas could also appear if gap patches were suitably distributed and migrations of centipedes between them and the nearby meadow were possible.

Niemelä *et al.* (1996) investigated communities of carabids, ants and spiders in boreal forest and found a clear difference in community composition among different forest age classes. It is likely in our case that the majority of predator species of the whole community were found in all forest age classes.

Bark beetle communities in different successional stages of subcontinental pine forests were investigated by Mokrzycki (1995). The species number rose with a stand's age. Schlyter & Lundgren (1993) found that managed forests with one age class favour defined bark beetle species of a narrower spectrum, which could reduce competition with other pests, predation and parasitism, and prevent healthy forest functioning.

In assessing differences between communities from different successional phases, authors mostly investigate stands that are evenly-aged over a large area, while in our study different phases are found in a small area within one unevenly-aged stand. We anticipate that centipede communities from evenly-aged stands of different phases would be significantly different than those from patches of different phases in an unevenly-aged stand. Investigation of different, evenly-aged stands in the same region (Grgič 2002) confirms this prediction, since greater differences among centipede communities were found. It is predicted that differences among centipede communities of different phases in a certain region depend on patch sizes and the distances between them.

Analysed communities from an unevenly-aged stand are richer and more similar in species number, compared to communities from evenly-aged stands in the same region (Kos 1996; Grgič 2002). In a certain development phase of an unevenly-aged stand, more species can occur than in an evenly-aged stand of the same phase. Migrations among patches could be the reason for such high species numbers and the density of centipedes.

The importance of horizontal stand structure for centipede diversity

In an evenly-aged stand only certain centipede species can occur. At the beginning of a forest's succession, a community of young forest develops and after that changes during the succession. Species for which conditions in a particular phase are suitable during the whole year will be present. Due to specific conditions, a lower number of species can exist in such stands. But in a stand with different development phases, species typical of different phases can occur. Specimens in such an environment can migrate between patches of different development phases, depending on current conditions, species characteristics, interspecies interactions and the characteristics of specimens. For their migration, a proper patch size and distribution is important. Such an unevenly-aged stand can offer favourable conditions for more centipede species, so it was predicted that alpha diversity and density is higher than it would be in an evenly-aged stand in the same area. In addition, a species that requires a certain phase can migrate during forest development according to the principle of metapopulation dynamics to a suitable new patch (e.g. Hanski & Gilpin 1997). In such an unevenly-aged stand, the matrix and distances are suitable for the migration of centipedes between patches. Similar results can also be expected for other poikilotherm organisms sensitive to environmental conditions. In an unevenly-aged stand, most species can find a patch with favourable conditions in every part of the year. Since the majority of animal species are poikilothermic and represent the biggest part of the biomass, they are vital for the existence of natural ecosystems.

A heterogeneous horizontal structure with mosaically distributed patches of different development phases and a high number of niches enable the existence of a large number of centipede species. Species easily migrate from one patch to another and increase diversity. The diversity of environments, species and genotypes in the landscape provides buffers against environmental fluctuations (Noss 1993). For biodiversity conservation and the stability of forest ecosystems, a horizontal structure with a suitable proportion, distribution and size of developmental phases is important. Many other authors (Noss 1993; Franklin 1993b; Neimelä *et al.* 1996; Bončina 2000) have similar opinions. Since small scale heterogeneity within a forest stand enhances local species richness and supports viable populations of specialised species, maintenance of this heterogeneity should be the key focus in management operations within a forest stand. A consensus has been reached among ecologists that an appropriate strategy for preserving diversity is to secure the heterogeneity of an environment at different scales simultaneously (Neimelä *et al.* 1996). Managers should be given detailed advice on what are the relevant scales of heterogeneity. An answer to this question requires widely extended investigations and inclusion of more taxa. But on the basis of our results we can state that the relevant scale for habitat heterogeneity is some tens of metres for centipedes and probably also for other forest-floor arthropods.

TABLE 3.

Percentage similarity estimates between centipede samples from different development phases in an unevenly-aged beech stand at Iška (Slovenia) in 2000.

PERCENTAGE SIMILARITY		***re-initiation phase***			***juvenile phase***			***pole phase***			***timber phase***		
		spring	*summer*	*autumn*	*spring*	*summer*	*autumn*	*spring*	*summer*	*autumn*	*spring*	*summer*	*autumn*
re-initiation phase	*spring*	100	76	67	74	73	62	78	70	66	71	72	62
	summer		100	74	57	69	63	67	56	60	78	80	74
	autumn			100	53	69	62	64	54	61	67	66	70
juvenile phase	*spring*				100	76	62	62	76	50	56	57	51
	summer					100	62	62	69	51	70	62	61
	autumn						100	65	52	58	63	58	66
pole phase	*spring*							100	58	72	68	65	55
	summer								100	58	55	52	50
	autumn									100	54	60	60
timber phase	*spring*										100	78	73
	summer											100	74
	autumn												100

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